appetite for grasshoppers, crickets, beetles, and caterpillars likely benefit gardeners and farmers, and one early explorer of the American west actually kept a pair of grasshopper mice in his basement as an effective form of 'cockroach control', opening the door to their cage each evening, closing the door when the mice returned, contentedly satiated, in the morning. And although still a long way off, the novel mechanism evolved by the mice for dealing with the intense and prolonged pain from a bark scorpion sting could lead to the development of a completely new class of analgesics, perhaps one lacking the unfortunate side effects of opiates — the benefits for people suffering chronic pain would be incalculable.

But maybe we should rethink the question. Most biologists consider *all* species 'good' in the sense that every plant, animal, fungus, virus, and bacterium is interesting and thus meritorious in its own right, worthy of our curiosity, investigation, and respect. Many species, if not most, may also play some critical role in their community we don't understand until it is too late — dodos, for example, appear to have been important to forest regeneration on Mauritius, while sea otters serve a keystone function promoting healthy kelp beds in the Pacific. Who knows what critical roles grasshopper mice might play in the deserts and grasslands they currently patrol, howling?

### *Where can I learn more about grasshopper mice?*

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## Quick guide

# Poison frogs

Jennifer L. Stynoski[1], Lisa M. Schulte[2], and Bibiana Rojas[3]

***What are poison frogs?*** Poison frogs, also commonly called 'dart poison frogs' or 'poison arrow frogs', are charismatic amphibians forming a spectacular adaptive radiation, comparable to that of African cichlids. Many of the diurnally active species have skin toxins and bright coloration (Figure 1), and display numerous terrestrial reproductive modes including elaborate parental care and complex social behaviors. The most diverse and well-studied group, superfamily Dendrobatoidea, consists of two families, Dendrobatidae and Aromobatidae, and is found from Nicaragua to northern South America. Although less popular, other groups known as poison frogs exist in South America (family Bufonidae, genus *Melanophryniscus*), Madagascar (family Mantellidae) and Australia (family Myobatrachidae, genus *Pseudophryne*), as well as two species in Cuba (family Eleutherodactylidae). Here, we focus on the traditional 'poison frogs', the dendrobatids.

***Are they called poison dart frogs, poison arrow frogs, dart-poison frogs, or just poison frogs?*** There are three species of poison frog (genus *Phyllobates*) to which common names including 'arrow' or 'dart' can be justly attributed. The epithet comes from the use that some Colombian native tribes made of these species' secretions, which when rubbed on darts provide a lethal hunting weapon. The exudate of a single golden arrow frog (*Phyllobates terribilis*) — one of the most toxic vertebrates — can kill up to six humans.

***Why are poison frogs interesting?*** Besides being poisonous, many species display bright colors and unique behaviors. Exceptional polymorphism and variation in coloration is due to both natural and sexual selection. Predator learning and recognition, as well as mating preferences in different species for novel, brighter, or familiar colors, have both played a role in producing a brilliant spectrum of color and pattern across the family. Coloration is an honest indicator of toxicity in some species, but not in others, and is associated with territorial aggressiveness and boldness in some cases. Recently, one Peruvian species, *Ranitomeya imitator*, was found to be a true Müllerian mimic of sympatric congeneric species. In addition, the males and females of several species are territorial and have particularly good orientation and homing ability. Male communication includes both acoustic (calls) and visual (vocal sac inflation) signals (Figure 1H); each of these signals is not as effective to repel intruders as the multimodal signal.

***How do they reproduce?*** Several species guard mates and some are completely monogamous. These strategies are associated with the most striking behavior observed in poison frogs: elaborate parental care. Parents guard terrestrial egg clutches and transport newly hatched tadpoles to water bodies (Figure 1G). Some species transport all tadpoles at once to small streams or puddles (Figure 1E,K). Other species transport tadpoles to very small pools in plants (phytotelmata; Figure 1C) where there is less predation risk (Figure 1F). Parents that place offspring in smaller pools generally transport tadpoles individually to separate pools to avoid competition for scarce food resources and even larval cannibalism (Figure 1B). Parents assess the quality and potential danger of tadpole deposition sites via chemical or visual cues. In some species, parental care goes a step further: after deposition, adults feed tadpoles with unfertilized eggs. In addition to providing food in resource poor environments, this behavior supplies tadpoles with alkaloids to protect them from predators. Hungry tadpoles distinguish between mothers and predators using visual and tactile cues, and then proceed to communicate with mother frogs by vibrating vigorously (Figure 1I), which appears to stimulate egg laying. Parental care can be performed by mothers, fathers or both parents, depending on the species.

 


**Figure 1. Examples of diversity of coloration and behaviors in poison frogs.**
(A) Mating pair of *Dendrobates tinctorius* in French Guiana and (B) tadpole of the same species which was bitten by a cannibalistic conspecific; (C) *Excidobates mysteriosus* in a bromeliad; (D) Peruvian *Ranitomeya fantastica*; (E) male *Ameerega hahneli* transporting all his tadpoles at once; (F) male of the monogamous *R. imitator* transporting a single tadpole and (G) embryo of same species; (H) calling male *Oophaga granulifera*; (I) 'blue jeans' female *O. pumilio* (one of the many different color morphs of this species) and its tadpole begging for nutritive eggs; (J) *Allobates granti*, an example of a poison frog species that is not brightly coloured; (K);*Hyloxalus nexipus* transporting tadpoles to a stream; (L) *D. auratus* from Costa Rica.

***What do we know about the poison frogs' toxins?*** Like all terrestrial amphibians, poison frogs face predators such as birds, spiders, bats, and snakes. Poison frogs use toxic alkaloids as chemical defenses against predators. They sequester alkaloids from their diet of mostly mites and ants, and accumulate them in granular skin glands. To date, over 500 different alkaloids have been described in Dendrobatoidea, of which about two-thirds are unique to them. For example, batrachotoxin, the most toxic poison frog alkaloid, binds irreversibly to voltage-gated sodium channels in neuron- and muscle-cell membranes, causing permanent depolarization by sodium influx and thus paralysis, heart arrhythmia and ultimately cardiac arrest. Other less toxic alkaloids, such as histrionicotoxins, act as antagonists of nicotinic acetylcholine receptors at the neuromuscular junction, inhibiting signal transduction. Epipedobatine also acts on acetylcholine receptors, ultimately triggering the release of dopamine and norepinephrine; it was a promising candidate for a non-opioid analgesic, but is not suitable for humans because the pharmaceutical concentration is too similar to the lethal dose. Phantasmidine, a recently identified and more selective alkaloid might lead to useful pharmaceuticals.

***Are poison frogs endangered?*** Many species are indeed on the IUCN Red List of Threatened Species due in large part to devastation by habitat loss. Also, some populations have shown to be affected by the Chytrid fungus (*Batrachochytrium dendrobatidis*), which is contributing to amphibian declines worldwide. Today, dendrobatids are generally found in dense but isolated populations in the remaining forest patches throughout their natural ranges. Also, in the 1960s and 1970s, poison frogs became very popular among hobbyists in North America and Europe because of their beauty. For decades this pet trade has posed a serious threat to natural populations, as traders looking to sell new color variants extract countless frogs. International trade regulations and captive breeding efforts exist, but the illegal pet trade still places pressure on natural populations.

***What can we learn from poison frogs in the future?*** The study of these animals is brewing strong amidst a robust foundation of literature and an energetic research community. Exciting new work in poison frogs will incorporate collaborative and interdisciplinary perspectives to elucidate patterns and mechanisms of behavior and evolution. For example, we will likely see research on learning and memory in the context of parental care, the evolution of complex behavior, flexibility and constraints of local speciation and polymorphism, resistance and adaptation to emergent diseases and habitat disturbance, and cellular and physiological mechanisms that regulate poison sequestration, orientation, and communication.

### *Where can I find out more?*

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## Correspondence

# Is there any evidence for vocal learning in chimpanzee food calls?

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In their study "Vocal Learning in the Functionally Referential Food Grunts of Chimpanzees", Watson *et al.* [1] claimed that they "provide the first evidence for vocal learning in a referential call in non-humans". We challenge this conclusion, on two counts. For one, we are not convinced that the authors controlled for arousal (or at least they did not report such data); furthermore, the vocal characteristics of the two groups largely overlapped already at the beginning of the study. Accordingly, we also question the authors' claim that their finding "sheds new light on the evolutionary history of human referential words".

Firstly, Watson *et al.* [1] argue that "call structure was not tied to arousal as calls changed while preferences stayed stable". Given the theoretical and empirical basis for linking vocalization structure (especially aspects related to frequency) to affective states [2], we agree with the authors that controlling for arousal (degree of stimulation) is critical to their conclusion. The authors had investigated the structure of food grunts before and after an integration of individuals from a Safari Park in the Netherlands (BB) into a group of chimpanzees residing at the Edinburgh Zoo (ED). If the BB individuals were simply highly aroused by apples when they moved to Edinburgh compared to ED individuals, and if this arousal declined over time, any changes to BB calls would be best explained by simple habituation to a stimulus (apples).

Watson *et al.*'s [1] conclusion relies on equating arousal and preference, which is fallacious. To demonstrate how different these two are, imagine a human repeatedly offered his/her favorite food in a series of choice trials (the authors' measure of preference). Regardless of how stable preference for this food remains, this person is surely going to be more excited to have their favorite food for the first time in months than for the third time in a week. No data are presented on apple feeding rates that BB individuals experienced in the Netherlands vs Edinburgh. It is thus plausible that BB individuals have an established preference for apples that is maintained, while the apple feeding at Edinburgh Zoo nonetheless led to a reduced state of arousal over time. A higher level of arousal of BB individuals at the start of the study could also be related to more excitement or higher levels of stress due to feeding in new environments and social contexts. Either way, it is important to rule out changes in arousal as the simplest explanation for the results, by collecting data on other aspects of behavior, such as submissive or self-directed behaviors [3], and/or physiology.

Secondly, there is an issue with the interpretation of the data. Despite the significant interaction reported for year and group, we observed that only seven calls from three subjects (out of a total of 20 calls from seven subjects) of the BB group recorded at the beginning of the study fell outside two standard deviations of the mean of the ED group (Figure 1). In other words, the majority of calls did not differ in the first place, indicating that irrespective of their provenance, most subjects of both populations had always responded with the general same call type to the presentation of apples. Moreover, the pattern whereby BB group individuals give calls above the range of ED individuals does not convincingly converge when looking at the data (Figure 1) — the seven BB calls above the ED range before group integration (2010) become five calls above the ED range following integration (2013) — weak evidence at best. Obviously two groups of humans from different linguistic backgrounds would most likely have entirely different words for the same things, not vocalizations that largely overlap.

More generally, even if Watson *et al*. [1] can provide new data that rule

 